Bot. Gaz. 152(3):257–262. 1991.

0006-8071/91/5203-0006$02.00

ECOPHYSIOLOGICAL RESPONSES OF C_3 FORBS AND C_4 GRASSES TO DROUGHT AND RAIN ON A TALLGRASS PRAIRIE IN NORTHEASTERN KANSAS

CRAIG E. MARTIN, FRED S. HARRIS, AND FRANK J. NORMAN[1]

Department of Botany, University of Kansas, Lawrence, Kansas 66045-2106

Ecophysiological responses to drought and a 3-cm rain were measured in seven C_3 forb and five C_4 grass species on a tallgrass prairie in northeastern Kansas. In general, midday leaf water potentials and conductances increased after rain to a greater extent in the C_3 forbs, although exceptions occurred. In particular, the deeply rooted *Silphium laciniatum* showed little or no change in water potential and three of the five grass species exhibited no change in conductance. Although the above differences in species and life-form responses were noted, few of the species exhibited signs of severe stress at the height of the drought, emphasizing the degree to which both C_3 forbs and C_4 grasses are adapted to occasional severe droughts in the prairies of North America.

Introduction

In the tallgrass prairies of North America, the majority of C_4 species are grasses, while most of the C_3 plants are forbs (Dickinson and Dodd 1976; Waller and Lewis 1979; Ode et al. 1980). Plants with the C_4 photosynthetic pathway generally exhibit higher CO_2 uptake rates and, thus, higher water-use efficiencies (ratio of carbon gained to water lost), relative to most plants having the C_3 photosynthetic pathway (Black 1971, 1973; Edwards and Walker 1983). Although exceptions do exist (Caldwell et al. 1977; Kemp and Williams 1980), the results of most studies support this generalization.

Thus, C_4 grasses may be better adapted to withstand the periodic severe droughts that occur in the Great Plains (Thornthwaite 1941; Borchert 1950; Coupland 1958; Wilhite and Neild 1982; Sala et al. 1988). Such a prediction, however, is based on the assumption that the two groups of plants differ only in their photosynthetic pathway. This is untrue; forbs typically have larger leaves, thus intercepting more light and possibly reaching superoptimal temperatures, and they are usually more deeply rooted than are the grasses (Weaver 1954; Weaver and Albertson 1956). Therefore, the ecophysiological responses of these two groups of prairie plants to severe drought are not so easily predicted (Weaver and Albertson 1936, 1944, 1956; Albertson and Weaver 1942; Weaver 1954; Coupland 1958; Risser et al. 1981). Predictions are also complicated by the length of the drought period, air temperatures during drought, and the ability of the plant to lie dormant or die back when stressed.

Surprisingly few studies have included comparative data on in situ responses of prairie plants to varying soil moisture. Furthermore, nearly all of these studies excluded forbs in their measurements (Sala et al. 1981*a*, 1981*b*, 1988; Barnes and Harrison 1982; Knapp 1984, 1985*a*, 1985*b*; Barnes 1985; Monson et al. 1986). In one such comparative study, predawn leaf water potential was measured in three C_3 forbs and four C_4 grasses during a drought year (1980) in a central Oklahoma tallgrass prairie (Hake et al. 1984). Although all species exhibited signs of drought stress, the grasses had lower water potentials in mid- and late summer. These results appear to indicate that the C_3 forbs were less affected by the drought conditions than were the C_4 grasses.

This study was initiated at the height of one of the longest periods of minimal precipitation during the 1988 drought, which was one of the worst in the century (Anonymous 1988). Midday leaf water potentials and conductances to water loss were measured in seven C_3 forbs and five C_4 grasses in a tallgrass prairie remnant in northeastern Kansas in order to compare the degree of stress, and subsequent recovery, among several species of C_3 forbs and C_4 grasses.

Material and methods

Study site

All measurements were taken on the Rockefeller Native Prairie, Nelson Environmental Study Area, Kansas Ecological Reserves (Fitch and Hall 1978). This tract, located approximately 13 km northeast of Lawrence, Kans., is a 4-ha tallgrass prairie, bordered by an eroded, degenerated prairie on one side and forest on all other sides. The prairie has never been plowed and is managed to reduce the invasion of weedy species by burning every 2–3 yr and by selective removal of

[1] Current address: Black and Veatch, 11401 Lamar Street, Overland Park, Kansas 66211.

Manuscript received January 1991; revised manuscript received April 1991.

Address for correspondence and reprints: Craig E. Martin, Department of Botany, University of Kansas, Lawrence, Kansas 66045-2106.

TABLE 1

SPECIES, FAMILY, AND LIFE-FORM
(including photosynthetic pathway, according to WALLER and LEWIS [1979])

Species	Family	Life-form
Silphium laciniatum L.	Asteraceae	C_3 forb
Helianthus rigidus (Cass.) Desf.	Asteraceae	C_3 forb
Solidago canadensis L.	Asteraceae	C_3 forb
S. rigida L.	Asteraceae	C_3 forb
Eryngium yuccifolium Michx.	Apiaceae	C_3 forb
Lespedeza capitata Michx.	Fabaceae	C_3 forb
Ceanothus americanus L.	Rhamnaceae	C_3 shrub
Andropogon gerardii Vitman	Poaceae	C_4 grass
A. scoparius Michx.	Poaceae	C_4 grass
Panicum virgatum L.	Poaceae	C_4 grass
Sorghastrum nutans (L.) Nash	Poaceae	C_4 grass
Tripsacum dactyloides (L.) L.	Poaceae	C_4 grass

woody species. On occasion, variations in this treatment regime have occurred. Most of the species included in this study (table 1) constitute the dominant species of this prairie. Species nomenclature follows that of GREAT PLAINS FLORA ASSOCIATION (1986). All plants were mature; some of the forbs were flowering.

The soil at the prairie site is a well-drained, fine-textured glacial till in the Pawnee series (SOIL CONSERVATION SERVICE 1977). Mean minimum and maximum air temperatures over the period 1951–1980 ranged from a low of −7.4 C in January to a summer maximum of 32.9 C in July. Annual precipitation over this same period averaged 93.5 cm. These environmental data were collected at the University of Kansas in Lawrence.

ENVIRONMENTAL CONDITIONS DURING MEASUREMENTS

Leaf water potentials were measured at the height of a severe drought on June 24, 1988, and after a substantial rain on July 1, 1988. Prior to the first date, a total of 0.33 cm of rain fell on two occasions in June (1–2 and 15), 8.00 cm on four occasions in May, and 6.98 cm on five occasions in April. Three days prior to the second set of measurements, 3.00 cm of rain fell at the site. Data on rainfall were collected at the Nelson Environmental Study Area; the rain gauge was approximately 2 km from the prairie site. Although no soil moisture measurements were made, the soil surface was extremely dry with large (up to 2-cm) cracks on June 24, 1988, and moist on July 1, 1988. It should be noted that, before the rain on June 28, the total precipitation since January was 28 cm below normal.

Days selected for measurements were mostly clear (photosynthetic photon flux density, measured by LI-COR [Lincoln, Nebr.] LI-190SB sensor and LI-185B meter, ranged from 1,500 to 1,800 μmol m^{-2} s^{-1}), with occasional small clouds that obscured the sun for brief periods. Measurements were taken between 1000 and 1500 h on both days. Air relative humidity at the beginning of the measurements was 30%–45%; air temperatures were cooler on the second date (see fig. 2 legend).

EXPERIMENTAL PROTOCOL

Leaf water potentials and conductances were measured simultaneously for each species, though not necessarily using the same plants for both types of measurements. Likewise, different individuals were measured on the two different dates. All individuals of a species ($N = 9$–13) were measured within a 10–30-min period, and the species were measured in the same order on the two sampling dates. In an attempt to account for any effect of time of day on the data, *Silphium laciniatum* was measured at the beginning and again at the end of the measurement period on both days; some differences were noted (figs. 1, 2).

DETERMINATION OF LEAF WATER POTENTIAL

Leaves were detached with a razor blade, placed in a plastic bag containing a moist paper towel, and then inserted into a rubber bung, which was subsequently pressurized in a pressure chamber (PMS Instruments, Corvallis, Oreg.) for measurement of xylem pressure potential, an estimate of leaf water potential (SCHOLANDER et al. 1965). The chamber was lined with wet paper towels to avoid tissue desiccation during the measurement (MERON et al. 1987). Measurements were always started within 1 min of leaf excision. Leaves of *Helianthus rigidus* released a viscous substance before xylem sap was expressed; the latter was taken as the pressure potential reading. Leaves of *S. laciniatum* were trimmed to allow insertion into the pressure chamber bung; the major vein and surrounding centimeter of tissue at the site of excision were not recut, avoiding underesti-

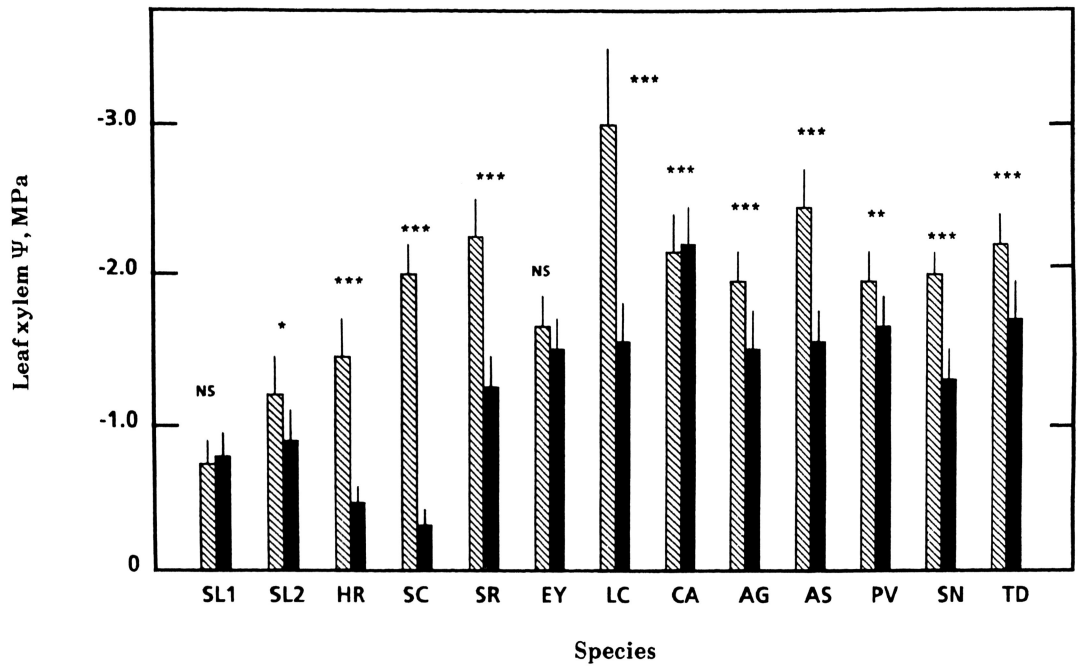

FIG. 1.—Leaf xylem water potential of 12 tallgrass prairie species in northeastern Kansas during (striped bar) and after (solid bar) an extremely dry period during the 1988 drought. Values are means with 1 SD; $N = 9$–12. Differences between each pair of means denoted as NS (not significant), * ($P < .05$), ** ($P < .01$), and *** ($P < .001$), according to the Student's t-test for all pairs except HR and SC, where the Mann-Whitney U-test was used. Species abbreviations are: SL = *Silphium laciniatum* (1 = before all measurements, 2 = after all measurements), HR = *Helianthus rigidus*, SC = *Solidago canadensis*, SR = *S. rigida*, EY = *Eryngium yuccifolium*, LC = *Lespedeza capitata*, CA = *Ceanothus americanus*, AG = *Andropogon gerardii*, AS = *A. scoparius*, PV = *Panicum virgatum*, SN = *Sorghastrum nutans*, and TD = *Tripsacum dactyloides*. The first seven species are C_3 forbs (CA = shrub); the last five are C_4 grasses.

mation of xylem pressure potential (SCHOLANDER et al. 1965).

DETERMINATION OF LEAF CONDUCTANCE

All leaves were measured in their natural orientation, attached to the plant, with a LI-COR LI-700 Transient Porometer (KANEMASU 1975). Conductances were measured on the abaxial side of all leaves; leaves were positioned in the cuvette so as to completely cover the slot inside. The porometer was calibrated at the start of measurements each day and whenever the cuvette temperature changed by 5 C. The calibration plate supplied with the instrument and distilled water were used for the calibrations.

The central portion of each leaf was used for measurement; distal tips were used for *S. laciniatum*. Healthy, mature leaves from the middle or upper portion of the shoot were selected for measurements.

STATISTICAL ANALYSES

All data were tested for normality and homoscedasticity. If a data set failed either test, nonparametric statistics were used. Pairs of means (during and after drought [figs. 1, 2]) were compared using the Student's t-test (parametric) or Mann-Whitney U-test (nonparametric). Larger groups of means (fig. 3) were compared with an analysis of variance (NESTAN) followed by a pairwise multiple comparisons-of-means (MCPAIR) test (parametric), or with a Kruskal-Wallis (KRWALL) test followed by a sum of squares (SSSTP) test (nonparametric). All methods were according to SOKAL and ROHLF (1981); the computer software package was that of ROHLF (1985).

Results and discussion

In all but three instances, midday leaf water potentials, as estimated by determinations of xylem pressure potentials, increased after the June 28 rain (fig. 1). This was also reflected in increases in leaf conductance to water loss in all but three cases (fig. 2). Those species that did not exhibit increases in conductance (three of the five grasses) were not the same as the three that lacked increases in leaf water potential (all C_3 species). Thus, all species examined in this study exhibited some indication of improved water status, either by an increase in water potential and/or an increase in conductance, following the rain. These results indicate that at the height of the severe drought all species were drought-stressed to some degree.

In spite of the severity of the drought (ANONYMOUS 1988), all plants investigated exhibited mean midday water potentials of −3.0 MPa or higher (fig. 1). Similar values were obtained be-

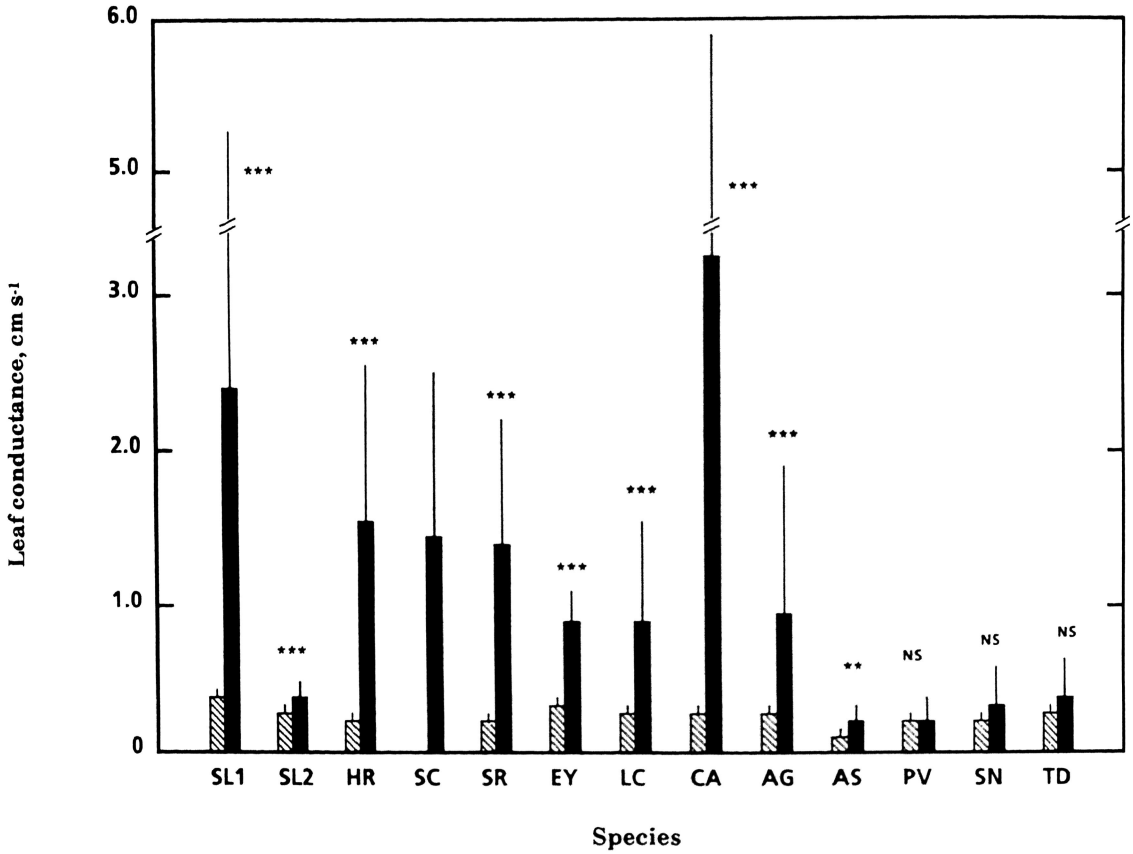

FIG. 2.—Leaf conductance to water loss of 12 tallgrass prairie species in northeastern Kansas during (striped bar) and after (solid bar) an extremely dry period during the 1988 drought. Values are means with 1 SD; $N = 9$–13. Differences between each pair of means denoted as NS (not significant), ** ($P < .01$), and *** ($P < .001$), according to the Mann-Whitney U-test for all pairs except SL2 and AS, where the Student's t-test was used. SC could not be tested, as conductances of all plants during the drought were zero. Species information is given in fig. 1 legend. Mean (± standard deviation; $N = 10$–13) cuvette temperatures upon measurement of conductance during drought ranged from 32.0 C (± 0.5) to 39.0 C (± 0.7); after the rain, means ranged from 29.9 C (± 0.7) to 36.1 C (± 0.8).

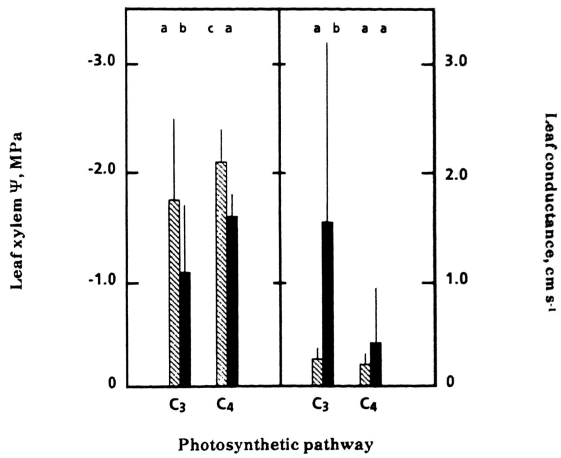

FIG. 3.—Leaf xylem water potential and conductance to water loss of seven C_3 species and five C_4 grasses in a tallgrass prairie in northeastern Kansas during (striped bar) and after (solid bar) an extremely dry period during the 1988 drought. Values are means with 1 SD; $N = 77$–78 for the C_3 plants, 50–54 for the C_4 plants. Means sharing the same letter are not significantly different ($P < .05$), according to analysis of variance and the MCPAIR test for the water potential data, and the KRWALL and SSSTP tests for the conductance data.

fore sunrise for prairie grasses and forbs during a year of drought in Oklahoma (HAKE et al. 1984). In addition, midday leaf water potentials of several of the grass species included in the current study have been measured at much lower values, down to −7.0 MPa (KNAPP 1984). Thus, although comparative data are few, it appears that the species in this study were suffering only moderate drought stress.

Ecophysiological measurements were made over a 5-h period at presumably the most stressful time of day (1000–1500 h). Leaf water potential and conductance were measured at the beginning and end of this period only with *Silphium laciniatum*. While only small changes in water potential throughout the course of measurements were noted, leaf conductances of plants examined after the rain decreased dramatically over the time of measurements. Data from the other species, albeit different species were compared at the different times, do not exhibit this trend (data not shown). These results may be explained by previous findings that photosynthetic CO_2 exchange

and stomatal conductance of *S. laciniatum* are particularly sensitive to midday stress resulting from high air temperature and vapor pressure deficit (JURIK et al. 1990). No other C_3 species exhibited such low conductances after the rain (fig. 2), regardless of the time of day at which measurements were made.

The only species that exhibited zero conductance, indicative of complete stomatal closure, during the drought was *Solidago canadensis* (fig. 2). Its water potential was also quite low (fig. 1). Both ecophysiological measures of water status responded dramatically to the rain, suggesting alleviation of stress.

Ceanothus americanus exhibited an unusual response to the droughted and nondroughted conditions. Unlike all other species, its leaf water potential was lower after the rain (fig. 1), yet the difference, although statistically highly significant, is so slight (0.03 MPa) as to be of questionable biological significance. In spite of this change, or lack thereof, leaf conductance in this woody prairie species increased nearly tenfold (fig. 2). Thus, it appears likely that this plant was drought-stressed before the rain; its water potential was low and stomata nearly closed. After the drought, however, leaf water potential remained low, accompanied by a very high conductance. These findings would be expected if high xylem tensions resulted from the high transpiration rates that necessarily accompanied the extremely high conductances found in this species.

Leaf water potentials in *S. laciniatum* and *Eryngium yuccifolium* increased only slightly or not at all after cessation of drought (fig. 1). Leaf conductances, on the other hand, increased after the rain in a similar manner as in the other C_3 species (fig. 2). The minor responses of leaf water potential to the drought in *S. laciniatum* may reflect its reported rooting depth of up to 5 m (WEAVER 1954). The rooting depth of *E. yuccifolium* has not been investigated. In this regard, it is interesting to note that *S. laciniatum* was one of the species least affected by the severe drought in the 1930s (WEAVER et al. 1935).

In general, leaf conductances of the C_4 grasses were lower than those of the C_3 forbs (figs. 2, 3). This is a common finding in comparisons of C_3 and C_4 plants (BLACK 1971, 1973; EDWARDS and WALKER 1983). Unlike the C_3 forbs, three of the five grass species examined showed no change in conductance (fig. 2) after the rain on June 28, though all five species exhibited small but significant increases in leaf water potential (fig. 1).

The comparative responses of the C_3 forbs and C_4 grasses to drought and to rain indicated that both sets of plants exhibited significant increases in leaf water potential, though only the C_3 species, as a group, also showed significant increases in conductance after the rain (fig. 3). Furthermore, changes in leaf water potential appeared greater in the C_3 species. The high variability in these data reflected the large increases in leaf water potential after the rain found in some, but not all, individuals, as well as species. In contrast, all C_4 species exhibited relatively small changes in leaf water potential. The study by HAKE et al. (1984) yielded opposite results from an Oklahoma prairie during a summer drought. Only predawn water potentials were measured in their study, however, making comparison of the two studies difficult. The results of the current study are suggestive that severe droughts are potentially more detrimental to C_3 forbs, except perhaps some species with extremely deep root systems, relative to C_4 grasses. Further data are necessary to substantiate or refute this tentative conclusion. Regardless, based on findings of this and other studies, it is clear that both C_3 forbs and C_4 grasses are well adapted to surviving occasional severe droughts in grasslands of the Great Plains.

Acknowledgments

We gratefully acknowledge the critical comments of VALERIE S. LOESCHEN; assistance in assembling precipitation data from GALEN PITTMAN and STEVE HAMBURG; as well as the skillful word processing of JAN ELDER and JUDY WIGLESWORTH.

LITERATURE CITED

ALBERTSON, F. W., and J. E. WEAVER. 1942. History of the native vegetation of western Kansas during seven years of continuous drought. Ecol. Monogr. **12**:23–51.

ANONYMOUS. 1988. 1980s: a decade of drought. Soil Water Conserv. News **9**(9):6–9.

BARNES, P. W. 1985. Adaptation to water stress in the big bluestem–sand bluestem complex. Ecology **66**:1908–1920.

BARNES, P. W., and A. T. HARRISON. 1982. Species distribution and community organization in a Nebraska sandhills mixed prairie as influenced by plant/soil-water relationships. Oecologia **52**:192–201.

BLACK, C. C. 1971. Ecological implications of dividing plants into groups with distinct photosynthetic production capacities. Adv. Ecol. Res. **7**:87–114.

———. 1973. Photosynthetic carbon fixation in relation to net CO_2 uptake. Annu. Rev. Plant Physiol. **24**:253–286.

BORCHERT, J. R. 1950. Climate of the central North American grasslands. Ann. Assoc. Am. Geogr. **40**:1–39.

CALDWELL, M. M., R. S. WHITE, R. T. MOORE, and L. B. CAMP. 1977. Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. Oecologia **29**:275–300.

COUPLAND, R. 1958. The effect of fluctuations in weather upon the grasslands of the Great Plains. Bot. Rev. **5**:274–317.

DICKINSON, C. E., and J. L. DODD. 1976. Phenological pattern in the shortgrass prairies. Am. Midl. Nat. **96**:367–378.

EDWARDS, G., and D. A. WALKER. 1983. C_3, C_4: mecha-

nisms, and cellular and environmental regulation, of photosynthesis. Blackwell, Oxford. 542 pp.

FITCH, H. S., and E. R. HALL. 1978. A 20-year record of succession on reseeded fields of tallgrass prairie on the Rockefeller Experimental Tract. Museum of Natural History Special Publication no. 4. University of Kansas Publications, Lawrence. 15 pp.

GREAT PLAINS FLORA ASSOCIATION. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence. 1,392 pp.

HAKE, D. R., J. POWELL, J. K. MCPHERSON, P. L. CLAYPOOL, and G. L. DUNN. 1984. Water stress of tallgrass prairie plants in central Oklahoma. J. Range Manage. **37**:147–151.

JURIK, T. W., H. ZHANG, and J. M. PLEASANTS. 1990. Ecophysiological consequences of nonrandom leaf orientation in the prairie compass plant, *Silphium laciniatum*. Oecologia **82**:180–186.

KANEMASU, E. T. 1975. The porometer of Kanemasu, Thurtell, and Tanner. Wash. State Univ. Coll. Agric. Res. Cent. Bull. no. 809. Pp. 17–20.

KEMP, P. R., and G. J. WILLIAMS III. 1980. A physiological basis for niche separation between *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4). Ecology **61**:846–858.

KNAPP, A. K. 1984. Water relations and growth of three grasses during wet and drought years in a tallgrass prairie. Oecologia **65**:35–43.

———. 1985*a*. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology **66**:1309–1320.

———. 1985*b*. Early season production and microclimate associated with topography in a C_4 dominated grassland. Acta Oecol. Oecol. Plant. **6**:337–346.

MERON, M., D. W. GRIMES, C. J. PHENE, and K. R. DAVIS. 1987. Pressure chamber procedures for leaf water potential measurements of cotton. Irrig. Sci. **8**:215–222.

MONSON, R. K., M. R. SACKSCHEWSKY, and G. J. WILLIAMS. 1986. Field measurements of photosynthesis, water-use efficiency, and growth in *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) in the Colorado shortgrass steppe. Oecologia **68**:400–409.

ODE, D. J., L. L. TIESZEN, and J. C. LERMAN. 1980. The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. Ecology **61**:1304–1311.

RISSER, P. G., E. C. BIRNEY, H. D. BLOCKER, S. W. MAY, W. J. PARTON, and J. A. WIENS. 1981. The true prairie ecosystem. Hutchinson Ross, Stroudsburg, Pa. 557 pp.

ROHLF, F. J. 1985. BIOM: a package of statistical programs to accompany the text Biometry. F. J. Rohlf, Stony Brook, N.Y. 84 pp.

SALA, O. E., W. K. LAUENROTH, W. J. PARTON, and M. J. TRLICA. 1981*a*. Water status of soil and vegetation in a shortgrass steppe. Oecologia **48**:327–331.

SALA, O. E., W. K. LAUENROTH, and C. P. P. REID. 1981*b*. Water relations—a new dimension for niche separation between *Bouteloua gracilis* and *Agropyron smithii* in North American semi-arid grasslands. J. Appl. Ecol. **19**:647–657.

SALA, O. E., W. J. PARTON, L. A. JOYCE, and W. K. LAUENROTH. 1988. Primary production of the central grassland region of the United States. Ecology **69**:40–45.

SCHOLANDER, P. F., H. T. HAMMEL, E. D. BRADSTREET, and E. A. HEMMINGSEN. 1965. Sap pressure in vascular plants. Science **148**:339–346.

SOIL CONSERVATION SERVICE. 1977. Soil survey of Jefferson County, Kansas. USDA, Washington, D.C.

SOKAL, R. R., and F. J. ROHLF. 1981. Biometry. 2d ed. Freeman, San Francisco. 859 pp.

THORNTHWAITE, C. W. 1941. Climate and settlement in the Great Plains. U.S. Dept. Agric. Yearbook **1941**:177–187.

WALLER, S. S., and J. K. LEWIS. 1979. Occurrence of C_3 and C_4 photosynthetic pathways in North American grasses. J. Range Manage. **32**:12–28.

WEAVER, J. E. 1954. North American prairie. Johnsen, Lincoln, Nebr. 348 pp.

WEAVER, J. E., and F. W. ALBERTSON. 1936. Effects of the great drought on the prairies of Iowa, Nebraska, and Kansas. Ecology **17**:567–639.

———. 1944. Nature and degree of recovery of grassland from the great drought of 1933 to 1940. Ecol. Monogr. **14**: 393–479.

———. 1956. Grasslands of the Great Plains. Johnsen, Lincoln, Nebr. 395 pp.

WEAVER, J. E., L. A. STODDART, and W. NOLL. 1935. Response of the prairie to the great drought of 1934. Ecology **16**:612–629.

WILHITE, D. A., and R. E. NEILD. 1982. Determining drought frequency and intensity on the basis of plant response: wild hay in the Sand Hills of Nebraska, U.S.A. Agric. Meteorol. **25**:257–265.